On the Importance of Shrub Encroachment by Sprouters, Climate, Species Richness and Anthropic Factors for Ecosystem Multifunctionality in Semi-arid Mediterranean Ecosystems

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Abstract

One of the most important changes taking place in drylands worldwide is the increase of the cover and dominance of shrubs in areas formerly devoid of them (shrub encroachment). A large body of research has evaluated the causes and consequences of shrub encroachment for both ecosystem structure and functioning. However, there are virtually no studies evaluating how shrub encroachment affects the ability of ecosystems to maintain multiple functions and services simultaneously (multifunctionality). We aimed to do so by gathering data from ten ecosystem functions linked to the maintenance of primary production and nutrient cycling and storage (organic C, activity of β-glucosidase, pentoses, hexoses, total N, total available N, amino acids, proteins, available inorganic P, and phosphatase activity), and summarizing them in a multifunctionality index (M). We assessed how climate, species richness, anthropic factors (distance to the nearest town, sandy and asphalted road, and human population in the nearest town at several historical periods) and encroachment by sprouting shrubs impacted both the functions in isolation and M along a regional (ca. 350 km) gradient in Mediterranean grasslands and shrublands dominated by a non-sprouting shrub. Values of M were higher in those grasslands and shrublands containing sprouting shrubs (43 and 62%, respectively). A similar response was found when analyzing the different functions in isolation, as encroachment by sprouting shrubs increased functions by 2–80% compared to unencroached areas. Encroachment was the main driver of changes in M along the regional gradient evaluated, followed by anthropic factors and species richness. Climate had little effects on M in comparison to the other factors studied. Similar responses were

observed when evaluating the functions in isolation. Overall, our results showed that *M* was higher at sites with higher sprouting shrub cover, longer distance to roads and higher perennial plant species richness. Our study is the first documenting that ecosystem multifunctionality in shrublands is enhanced by encroaching shrubs differing in size and leaf attributes. Our findings reinforce the idea that encroachment effects on ecosystem functioning cannot be generalized, and that are largely dependent on the traits of the encroaching shrub relative to those of the species being replaced.

Key words: shrub invasion; ecosystem structure; ecosystem functioning; biodiversity; drylands; *Quercus coccifera*; *Rosmarinus officinalis*; *Stipa tenacissima*.

Introduction

Drylands, regions with an aridity index (precipitation/potential evapotranspiration) value lower than 0.65 (UNCCD 1992), cover over 40% of the Earth's surface, provide key ecosystem services to more than 38% of the global human population (MEA 2005), and include highly diverse biomes that host about 20% of the major centers of plant diversity worldwide (White and Nackoney 2003; Kier and others 2005). One of the most important changes taking place in these regions over the last 150 years is shrub encroachment, that is, the increase of the cover and dominance of shrubs in areas formerly devoid of them, such as grasslands (van Auken 2009; Naito and Cairns 2011). Numerous papers have dealt with the causes and consequences of shrub encroachment for both ecosystem structure and functioning (see van Auken 2009 and Eldridge and others 2011 for recent reviews). The ecological consequences of shrub encroachment are not universal (Eldridge and others 2011), and the effects of this phenomenon on ecosystems range from negative to positive, depending on the region considered, the ecosystem function/s of interest and the organisms studied (Cable and others 2009; Jackson and others 2002; Maestre and others 2009; Ratajczak and others 2012).

The differences found in the literature between regions and ecosystem types regarding the ecological consequences of shrub encroachment may be due to the attributes of encroachers. Maestre and others (2009) hypothesized that the effects of shrub encroachment on ecosystem functioning are partially due to a set of key traits of potential encroachers relative to that of the grasses they replace. Eldridge and others (2011) tested this prediction indirectly, by using data available in the literature, and found support for these predictions, as traits such as the height and shape of the shrubs affected the structural and functional outcomes of their encroachment. However, and to the best of our knowledge, no previous study has directly evaluated in the field how the nature of encroaching shrubs relative to those of the species being replaced modulate their effects on ecosystem functioning. This kind of studies may shed some light on the variable ecological effects of encroaching shrubs found in literature.

Most of the previous research evaluating the effects of shrub encroachment on ecosystem functioning has focused on evaluating only one or a few ecosystem functions at a time, such as productivity (Huenneke and others 2002), soil carbon and nitrogen contents (Jackson and others 2002; Wheeler and others 2007; Alberti and others 2011), and enzyme activities (Maestre and others 2011), to name a few. Although studies evaluating single variables are relevant, ecosystems are valued primarily for the multiple functions and services they provide (MEA 2005), and shrub encroachment can affect multiple structural and functional variables at the same time (Eldridge and others 2011). Therefore, assessing how this phenomenon affects multiple ecosystem functions and services simultaneously, that is, multifunctionality (Reiss and others 2009; Zavaleta and others 2010; Cardinale and others 2011), can provide greater insights on the ecological consequences of shrub encroachment, and help managers and policy makers to establish sound management actions. Although the evaluation of multifunctionality is becoming prevalent in areas of ecology such as biodiversity–function research (Hooper and Vitousek 1998; Hector and Bagchi 2007; Gamfeldt and others 2008; Maestre and others 2012a), only Eldridge and others (2011) have attempted to explore the effects of shrub encroachment on multifunctionality so far, and their study was conducted with data from published studies that primarily focused on particular structural and functional attributes. Therefore, there is a critical need for field studies evaluating the effects of shrub encroachment on multifunctionality.

Although very important, shrub encroachment is not the only factor-affecting ecosystem functioning in drylands. Previous studies have found that abiotic factors such as temperature and precipitation, and biotic factors such as species richness, can modulate ecosystem functioning along regional or global gradients (Paruelo and others 2004; Wang and others 2011; Maestre and others 2012a). Anthropic factors, such as past human activities, have been traditionally overlooked when studying drivers of ecosystem functioning in drylands. These have been found to be a major driver of ecosystem structure in different ecosystems (Waide and others 1999; Maestre 2004), and their effects on ecosystem functions could be even stronger, given that impacts of human activities on nutrient cycling and pools may last from decades to millennia (Dupouey and others 2002; Kacalek and others 2011; De Schrijver and others 2012). Studying anthropic factors is particularly important in areas with a long history of human use, such as the Mediterranean Basin (Blondel 2006), and when evaluating the functional consequences of shrub encroachment, as this phenomenon is largely driven by human-driven factors such as the introduction of grazers (di Castri 1981; Seifan and Kadmon 2006), changes in the regime of wildfires (Pausas 2004), and climate change (Archer and others 1995).

We evaluated how climate, species richness, anthropic factors, and shrub encroachment by sprouting shrubs impacted ecosystem multifunctionality along a regional environmental gradient in semi-arid Mediterranean grasslands and shrublands. These landscapes are ideal ecosystems to do so, as both past human uses and shrub encroachment have been previously found to affect their structure and functioning (Maestre 2004; Maestre and others 2009). Mediterranean drylands are also suitable to test how the traits of the encroacher relative to those of the species being replaced affect the functional outcome of encroachment, because *Quercus coccifera* L., a large sprouting shrub is becoming more abundant at both grasslands dominated by the perennial grass *Stipa tenacissima* L. and shrublands dominated by the obligate-seeder *Rosmarinum officinalis* L. (supplementary Figure S1). Our first objective was to evaluate how increases in the cover and density of *Q. coccifera* affected multiple ecosystem functions (organic C, activity of β-glucosidase, pentoses, hexoses, total N, total available N, amino acids, proteins, available inorganic P, and phosphatase activity), both in isolation and when evaluated simultaneously (that is, multifunctionality), in both *S. tenacissima* grasslands and *R. officinalis* shrublands. We hypothesized that the magnitude of changes on ecosystem functions and multifunctionality with sprouting shrubs will be higher in grasslands than shrublands. We expect so because sprouting shrub leaves have lower C:N ratios than those of *S. tenacissima* (García and others 2005), and these shrubs can promote the activity and abundance of bacteria and fungi compared to grasses (Azcón-Aguilar and others 2003; Maestre and others 2009). Furthermore, they have higher biomass, primary production and litter productivity than *S. tenacissima* (Cañellas and Miguel 1998, 2000; Maestre and others 2007), and shrubs like *R. officinalis* have increased litterfall compared to *S. tenacissima* (Bochet and others 1998). Overall, these changes may lead to higher nutrient contents and improved physical soil properties under shrub canopies than under grass canopies (Bochet and others 1999; Maestre and Cortina 2004; Castillo-Monroy and others 2010; supplementary Figure S2), maximizing the effects of encroachment by sprouting shrubs in *S. tenacissima* grasslands compared to *R. officinalis* shrublands. Our second objective was to evaluate the relative importance of sprouting shrubs, climate, anthropic effects, and plant species richness on the ecosystem functions evaluated and on multifunctionality. We thus postulate that higher aridity and species richness will decrease and increase multifunctionality, respectively (Miranda and others 2009; Maestre and others 2012a), and that anthropic effects will reduce multifunctionality. We expect so because of the negative impacts that traditional and current human activities such as grazing, wood, and fibber harvesting have on plant cover and species richness (Maestre 2004; Seifan and Kadmon 2006), and on processes such as erosion, nutrient cycling and storage (Tongway and others 2003; Bastida and others 2006).

Materials and Methods

Study Area and Experimental Design

We surveyed 44 sites located along an environmental gradient from central to SE Spain (supplementary Figure S3). The climate was semi-arid, with annual rainfall and temperature varying from 339 to 479 mm, and from 12.4 to 16.5°C, respectively (supplementary Table S1). All plots were located on *Lithic Calciorthid* (Soil Survey Staff 1994) soils. This study was conducted in either grasslands or shrublands dominated by *S. tenacissima* and *R. officinalis*, respectively. Within grasslands (GR) and shrublands (SH), we selected sites with and without sprouting shrubs (SP), having then four types

of communities, hereafter named as GR, GRSP, SH, and SHSP (n = 11 sites per group). The dominant sprouting shrub was *Q. coccifera* in all cases, except in a SH site, where the sprouters were young trees of *Quercus ilex* L., a species highly related to *Q. coccifera* (Pearse and Hipp 2009). There were no differences among the four vegetation types studied regarding abiotic factors such as aridity index and elevation (Two-way ANOVA, $F_{3,40} < 1.23$, $P > 0.31$ in all cases). Total cover ranged from 36 to 68% in grasslands, and from 15 to 64% in shrublands. Sprouting shrub cover did not differ between GRSP (means ± SE, 14 ± 3%) and SHSP (20 ± 4%) sites (Two-way ANOVA, $F_{1,20} = 1.66$, $P = 0.21$). Thus, we had similar environmental conditions within both types of landscape (that is, grasslands and shrublands) along the climatic gradient, and in both of them the sites with sprouting shrubs had similar cover values.

Composition and Structure of Vascular Plants: Biotic Factors

At each site, we established a 30 × 30 m^2 plot in an area representative of its overall vegetation. We assessed the cover of perennial vegetation using the line-intercept method in four 30-m long transects per plot, which were extended parallel to the slope and located 8 m apart. In each transect, we also placed 20 consecutive quadrats (1.5 × 1.5 m^2 size), where the cover of each perennial species was visually estimated. We restricted our study to perennial plants because they are instrumental in maintaining ecosystem functioning and preventing desertification in drylands (Whitford 2002; Maestre and Escudero 2009). The total number of perennial species found in the 80 quadrats was used as our surrogate for species richness per plot. With this information, we calculated an encroachment index per plot, defined as SPC − nSPC/TC, with SPC being the cover of sprouting shrubs, nSPC the cover of non-sprouting shrubs and TC the total vegetation cover. This index provides a numerical and continuous indicator of sprouting shrub cover, taking into account the cover of non-sprouting shrubs and the total cover per plot, to control the potential effect of both factors on our response variables across plots.

Abiotic, Climatic, Geographic, and Anthropic Variables

The coordinates of each plot were recorded in situ with a portable Global Positioning System (GPS), and were standardized to the WGS84 ellipsoid for visualization and analyses. GPS coordinates were used to obtain 21 standardized climatic variables from Worldclim (www.worldclim.org), a high resolution (30 arc s or ~1 km at equator) climate database (Hijmans and others 2005). We then conducted a principal component analysis (PCA) using a correlation matrix with the 21 climatic variables (supplementary Table S2). The three first components of this PCA (hereafter named *Clim-Ax1*, *Clim-Ax2*, *Clim-Ax3*) had eigenvalues higher than one, and thus were retained for further analyses (Quinn and Keough 2002); these axes explained 92.5% of variation in climatic data. *Clim-Ax1* was negatively related to isothermality [that is, (Mean Diurnal Range/Temperature Annual Range) (×100)], *Clim-Ax2* was positively and negatively related to annual precipitation and annual mean temperature, respectively, whereas *Clim-Ax3* was positively related to the average diurnal range in temperature [that is, Mean of monthly (max temp − min temp)] (supplementary Table S2). The slope angle of each plot was measured in situ with a clinometer.

We used the following variables as surrogates of human impacts at the experimental sites: distance to the nearest town, human population in the nearest town at several historical periods (1857, 1887, and 1950), distance to the nearest dirt road and distance to the nearest asphalted road. The Euclidean distance between the center of each plot and the center of the nearest town/city and asphalted/dirt road was obtained with Google Earth (www.google.com/earth/index.html). We assumed that the closer a given plot to the nearest city/town and dirt/asphalted road, the more likely that site was to have suffered from greater human impacts in the past (Calef and others 2008; Rogala and others 2011). Population dates were selected because they represent the first census per municipality available in Spain (1857), and two moments of special human pressure on natural resources because of the lack of woody fuel (1887) and the socio-economic situation following the Spanish Civil War (1950; Servicio del Esparto 1950; López and others 1992). Population data were obtained from official statistics (www.ine.es). We conducted a PCA using a correlation matrix with the different human variables selected. The three first components of this PCA (hereafter named *Anth-Ax1*, *Anth-Ax2*, *Anth-Ax3*) had eigenvalues higher than one, and thus were retained for further analyses (Quinn and Keough 2002); these axes explained approximately 79% of variation in anthropic data. *Ant-Ax1* was positively correlated to human population in the three dates (Pearson's $r > 0.70$ for the three

variables), *Ant-Ax2* was positively correlated to distance to the nearest asphalted road (Pearson's $r = 0.90$) and *Ant-Ax3* was positively correlated to distance to the nearest dirt road (Pearson's $r = 0.98$).

Assessment of Ecosystem Multifunctionality

Soil sampling and laboratory analyses were conducted as described in supplementary information S1. We evaluated ten soil variables (ecosystem functions hereafter) linked to the maintenance of primary production and nutrient cycling and storage (organic C, activity of β-glucosidase, pentoses, hexoses, total N, total available N, amino acids, proteins, available inorganic P, and phosphatase activity; see supplementary information S1 for a rationale of the variables employed). Although we also analyzed all these ecosystem functions separately, they were summarized in a multifunctionality index (M), calculated as the average of the Z scores of the ten ecosystem functions estimated at the plot level (Maestre and others 2012a; supplementary information S1). This index provides a straightforward and easily interpretable measure of multifunctionality. We acknowledge that, by using such an average, declines in one function can theoretically be compensated for by increases in one or another function (Gamfeldt and others 2008, 2013). However, we did not find that sites with high values of a single or a few functions had consistently low values for other functions. Indeed, the correlations between our ecosystem functions were either positive or close to 0 in most cases (supplementary Table S3). Therefore, the higher the M values, the higher the multifunctionality. Similarly, we also obtained functions from the N, C, and P cycles by averaging the Z scores of the variables involved in each cycle, which were named as N, C, and P indices, respectively. Indices such as those used here are increasingly used in the multifunctionality literature (for example, Zavaleta and others 2010; Mouillot and others 2011; Freudenberger and others 2012; Maestre and others 2012b; Bowker and others 2013), as they summarize and integrate the effects of multiple functions into a single metric that is easily interpretable and analyzable quantitatively. The multifunctionality indices employed here also have good statistical properties, as they follow a normal distribution (Kolmogorov–Smirnof tests, $P > 0.2$ for the four cases), and are highly related to other multifunctionality indices proposed in the literature (supplementary Figure S4).

Statistical Analyses

We first explored the effects of sprouting shrubs on the functions evaluated and on multifunctionality in both grasslands and shrublands by using two-way ANOVA, with landscape type (L, grassland vs. shrubland) and the presence/absence of sprouting shrubs (R) as main, fixed, factors. Results revealed a lack of interactions between both factors for M, and for C, N and P indices, as well as for every function evaluated but total available N, suggesting that encroachment had the same effects on shrublands and grasslands (Figures 1, 2; supplementary Tables S4 and S5). Given these results, we pooled data from both vegetation types for further analyses.

We followed a multi-model inference approach (Burnham and Anderson 2002), which uses information theory to assess the probability that a given model is the most appropriate description of the observed data (Johnson and Omland 2004). We evaluated all possible linear regression models containing the different functions evaluated, M, C, N, or P index as the dependent variable and the following independent variables: encroachment index, species richness, slope, climatic, and anthropogenic factors. Due to the limited number of sites that we have in this study ($n = 44$), we had to keep a unique climatic and anthropogenic PCA component to avoid problems related to overfitting and spurious effects (Burnham and Anderson 2002). Thus, we used the *Clim-Ax1* and *Anthr-Ax3* in our models, as they were the components most related to the M, C, N, and P indices, and to most of the functions evaluated (supplementary Table S6). The variance inflation factor between the independent variables included in our models was below four, suggesting the absence of colinearity problems (Chatterjee and Price 2001). Model selection criterion is described in supplementary information S2.

The characteristics of our survey make the presence of spatial autocorrelation likely, which may be a problem in multi-model approaches based on information theory (Hoeting and others 2006). To check the potential effects of spatial autocorrelation in the data, a Moran's I correlogram was done on the residuals of either ANOVAs or the best model from the multi-model analysis. ANOVA analysis was carried out with Statistica v7 software and correlograms and multi-model analyses were carried out with the SAM 4.0 software (Rangel and others 2010). The data used in this article are deposited in the Dryad repository: http://dx.doi.org/.

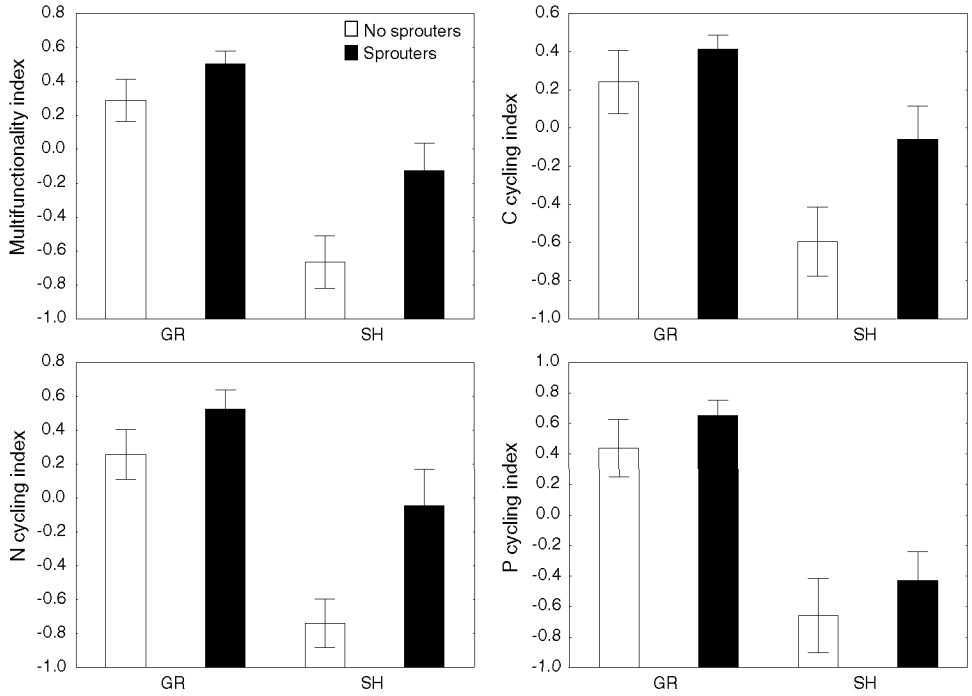

Figure 1. Effects of the presence of sprouting shrubs on multifuncionality (M), and on carbon (C), nitrogen (N), and phosphorous (P) cycling indices in grasslands (GR), and shrublands (SH). Data represent means ± SE (n = 11). ANOVA results for the data presented in this figure are shown in supplementary Table S4.

Results

The presence of sprouting shrubs increased *M*, *C*, *N*, and *P* indices (Figure 1, supplementary Table S4). This trend was followed for most of the ecosystem functions when analyzed separately (Figure 2, supplementary Table S5). Moran's I correlograms of residuals from ANOVA analyses showed a lack of spatial autocorrelation in the different response variables evaluated, suggesting that our results were not biased by spatial autocorrelation (supplementary Figure S5).

When considering predictor variables other than sprouting shrubs, results showed that the best (smallest AIC_c) and most parsimonious (fewest variables with AIC_c values comparable to those of the best model, that is, $AIC_c < 2$) models describing the multifunctionality index (*M*) contained three and two predictor variables, respectively (Table 1). Both models explained around 40% of the variance found in *M*, and included the encroachment index and the third anthropic PCA component (*Ant-Ax3*) as predictor variables. The best model also included plant species richness. On the contrary, the first climatic PCA component (*Clim-Ax1*) included neither the best nor the most parsimonious models explaining *M*, *C*, *N*, and *P* indices. Slope was also included in the best model explaining the *P* index. Residuals of the best four models did not suffer from spatial autocorrelation, as indicated by Moran's I correlograms (supplementary Figure S6). Similar results were found when ecosystem functions were separately analyzed (supplementary Table S7). Variables such as organic carbon, activity of β-glucosidase, total nitrogen or amino acid content included the encroachment index, plant species richness and the third anthropic PCA component (*Ant-Ax3*) as predictor variables in their most important models. Variables related to the P cycle such as available P similarly include slope in the best model explaining this variable. The encroachment index, the *Anth-Ax3* component and species richness were the most important predictors of *M* (Figure 3). The three independent variables were positively related to *M*, indicating that higher ecosystem functionality was found at those sites with higher cover of sprouting shrubs, longer distance to roads and higher species richness (Table 2). In addition, the *Clim-Ax1* component and slope had a low relative importance as predictors of *M* (Figure 3). The removal of *Anth-Ax3* as a predictor variable substantially reduced the fit of the model (Table 1). Thus, for the *M* index, the first and the second models of Table 1 are the best and the most parsimonious models, respectively; the same models without the *Ant-Ax3* component had $R^2 = 0.368$, $AIC_c = 70.95$, $\Delta AIC_c = 7.52$; and $R^2 = 0.276$, $AIC_c = 74.53$, $\Delta AIC_c = 5.09$, respectively.

Similar results were found when functions related to the C and N cycles (that is, *C* and *N* indices) were evaluated separately (Table 1). The encroachment index, the *Anth-Ax3* component and species richness were the most important predictors of *C* and *N* indices. In both cases, the relative importance of

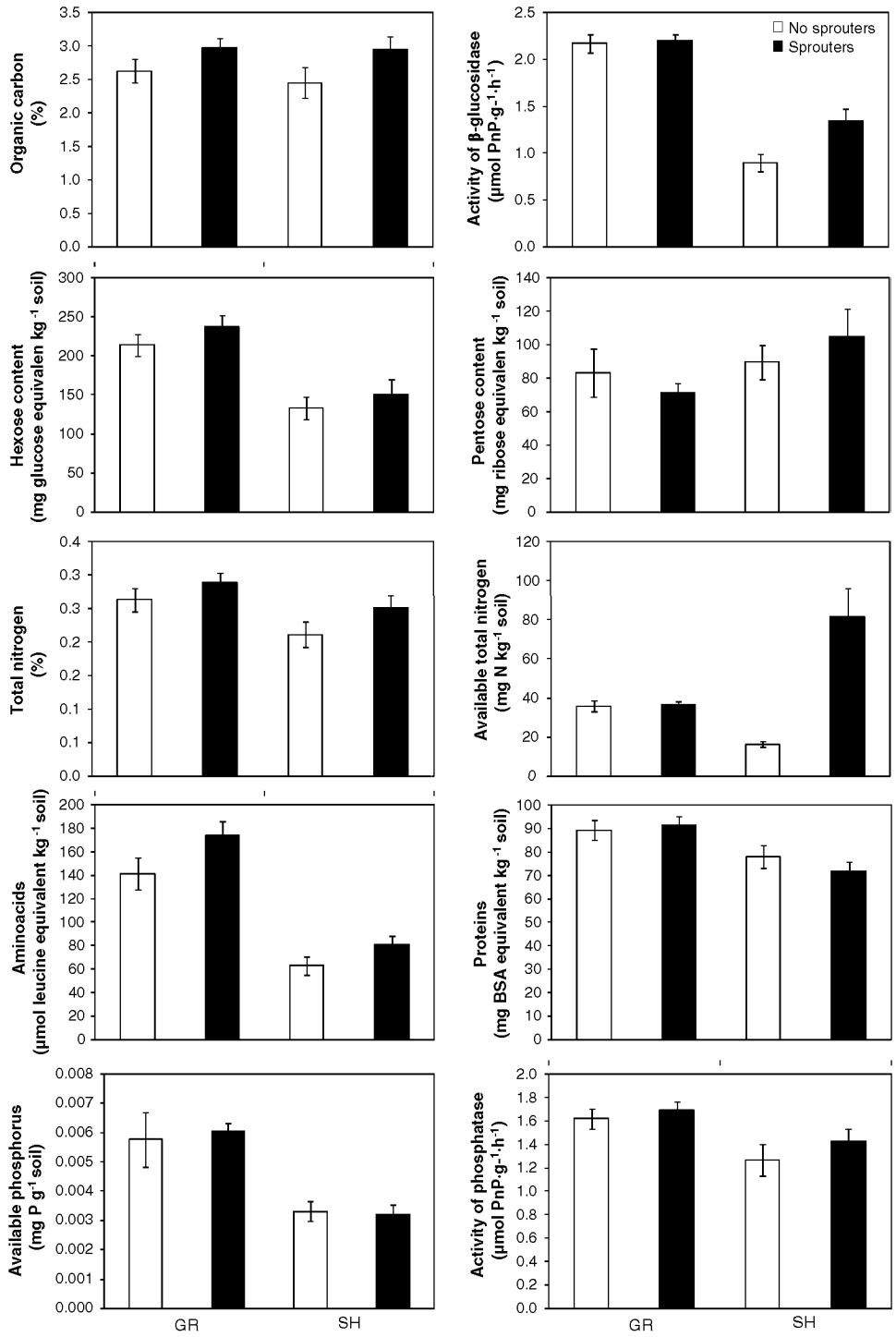

Figure 2. Effects of the presence of sprouting shrubs on the ten ecosystem functions studied in grasslands (GR) and shrublands (SH). Data represent means ± SE (n = 11). ANOVA results for the data presented in this figure are shown in supplementary Table S5.

the *Clim-Ax1* component and slope was low (Figure 3). The encroachment index, the *Anth-Ax3* component and species richness were positively related to *C* and *N* indices, meaning that higher ecosystem functionality related to C and N cycles was found at those sites with higher cover of sprouting shrubs, longer distances to roads, and higher species richness (supplementary Table S8). For the *C* index, the first model in Table 1 was the best and the most parsimonious model, and did not include the *Ant-Ax3* component. For the *N* index, the first and the second models in the table were the best and the most parsimonious models, respectively. For this index, the removal of the *Ant-Ax3* component only reduced the model fit in the second case (R^2 = 0.230, AIC_c = 87.024, ΔAIC_c = 5.11).

Table 1. Top Five Best-fitting Regression Models of Ecosystem Multifunctionality Using Ordinary Least Squares Regression

SR	Enc I	SLO	Clim-Ax1	Anth-Ax3	R^2	AICc	ΔAIC	Wi
M								
■	■			■	0.42	63.43	0	0.24
	■			■	0.39	69.44	0.01	0.23
■	■				0.37	70.95	1.52	0.11
■	■		■	■	0.43	71.87	2.44	0.07
	■	■		■	0.39	71.91	2.48	0.07
C								
■	■				0.31	75.69	0	0.22
■	■			■	0.34	76.53	0.85	0.14
	■			■	0.29	76.81	1.12	0.13
■	■		■		0.32	77.74	2.05	0.08
■	■	■			0.31	77.9	2.22	0.07
N								
■	■			■	0.40	81.29	0	0.23
	■			■	0.35	81.91	0.62	0.17
■	■				0.34	82.62	1.33	0.12
■	■		■	■	0.40	83.45	2.16	0.08
■	■	■		■	0.40	83.58	2.29	0.07
P								
	■	■		■	0.34	99.93	0	0.26
	■			■	0.29	100.55	0.62	0.19
■	■		■	■	0.34	102.38	2.45	0.08
	■	■			0.26	102.6	2.66	0.07
	■	■	■	■	0.34	102.6	2.67	0.07

Each column represents a different predictor variable (SR, perennial plant species richness; Enc I, encroachment index; SLO, slope; Clim-Ax1, first component of a principal-components analysis conducted with 21 climatic variables; Ant-Ax3, third component of a principal-components analysis conducted with the distance to the nearest town, the 1857, 1887 and 1950 population censuses of these towns and the distance to the closest dirty and asphalted road). AICc measures the relative goodness of fit of a given model; the lower its value, the more likely it is that this model is correct; ΔAICc is the difference between the AICc of each model and that of the best model; Wi are the Akaike weights. Unshaded cells indicate variables that were not included in a particular model.

The encroachment index, the *Anth-Ax3* component and slope were the most important predictors of the *P* index (Figure 3). The relative importance of the *Clim-Ax1* component and species richness was low (Figure 3). The encroachment index and the *Anth-Ax3* component were positively related to *P* index, and slope was negatively related to this index, meaning that higher ecosystem functional-

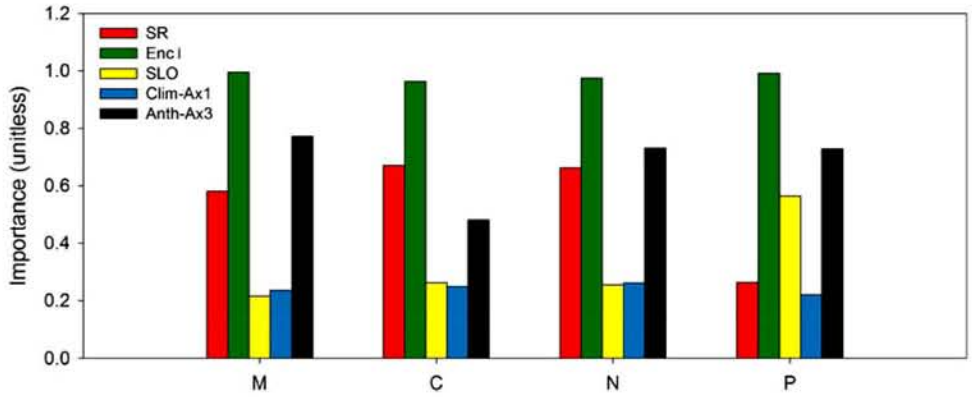

Figure 3. Relative importance of predictor variables in models of ecosystem multifunctionality (M) and carbon (C), nitrogen (N), and phosphorus (P) indices. The height of each bar is the sum of the Akaike weights (Wi) of all models that included the predictor of interest, taking into account the number of models in which each predictor appears. Variable abbreviations as in Table 1.

Table 2. Multi-model Averaged Parameter Estimates of the Analyses Conducted with the Multifunctionality Index (*M*) as Dependent Variable and All Possible Combinations of the Independent Variables Used

Variable	Coefficient	STE	SE	*t*	95% Lower CI	95% Upper CI
A						
SR	0.018	0.250	0.006	2.959	0.006	0.030
Enc I	0.678	0.507	0.175	3.867	0.334	1.021
SLO	0.001	0.015	0.003	0.510	-0.004	0.007
Cli-Ax1	0.011	0.043	0.009	1.175	-0.007	0.029
Ant-Ax3	0.183	0.296	0.064	2.867	0.058	0.309
B						
SR	0.015	0.205	0.009	1.549	-0.004	0.033
Enc I	0.671	0.503	0.164	4.094	0.35	0.993
Ant-Ax3	0.16	0.258	0.081	1.97	<0.001	0.318
C						
Enc I	0.723	0.542	0.163	4.432	0.404	1.042
Ant-Ax3	0.209	0.338	0.076	2.763	0.060	0.358

SR, perennial plant species richness; Enc I, encroachment index; SLO, slope; Clim-Ax1, first component of a principal-components analysis conducted with 21 climatic variables; Ant-Ax3, third component of a principal-components analysis conducted 6 variables related with anthropic factors. The results shown are the parameter estimates averaged across 31 models using Akaike weights and ordinary least square regression (A) and the parameters estimates for the best (that with the lowest AIC_c) and most parsimonious (fewest independent variables with $\Delta AIC < 2$) ordinary least squares models (B and C, respectively). STE = Standardized coefficient, SE = Standard error and CI = confidence intervals

ity related to P cycle was found at those sites with higher cover of sprouting shrubs, longer distances to roads and smoother sites (supplementary Table S8). The fit of the models adjusted to the *P* index was substantially reduced when removing the *Anth-Ax3* component as a predictor variable. The first and the second models in Table 1 were the best and the most parsimonious models, respectively for the *P* index; the same models without the *Ant-Ax3* component had $R^2 = 0.257$, $AIC_c = 102.59$, $\Delta AIC_c = 2.66$; and $R^2 = 0.213$, $AIC_c = 102.70$, $\Delta AIC_c = 2.15$, respectively.

Similarly to *M*, *C*, *N*, and *P* indices, functions analyzed separately showed similar results. The encroachment index was one of the most important predictors for all ecosystem functions but protein content. Species richness was also an important predictor for hexose, amino acid and protein contents, and the *Anth-Ax3* component was important for organic carbon, total nitrogen, total available nitrogen and phosphatase extracellular activity. Slope was an important predictor for available phosphorus (Figure 4).

Discussion

Given the extent of shrub encroachment worldwide, it is not surprising to find an increasing

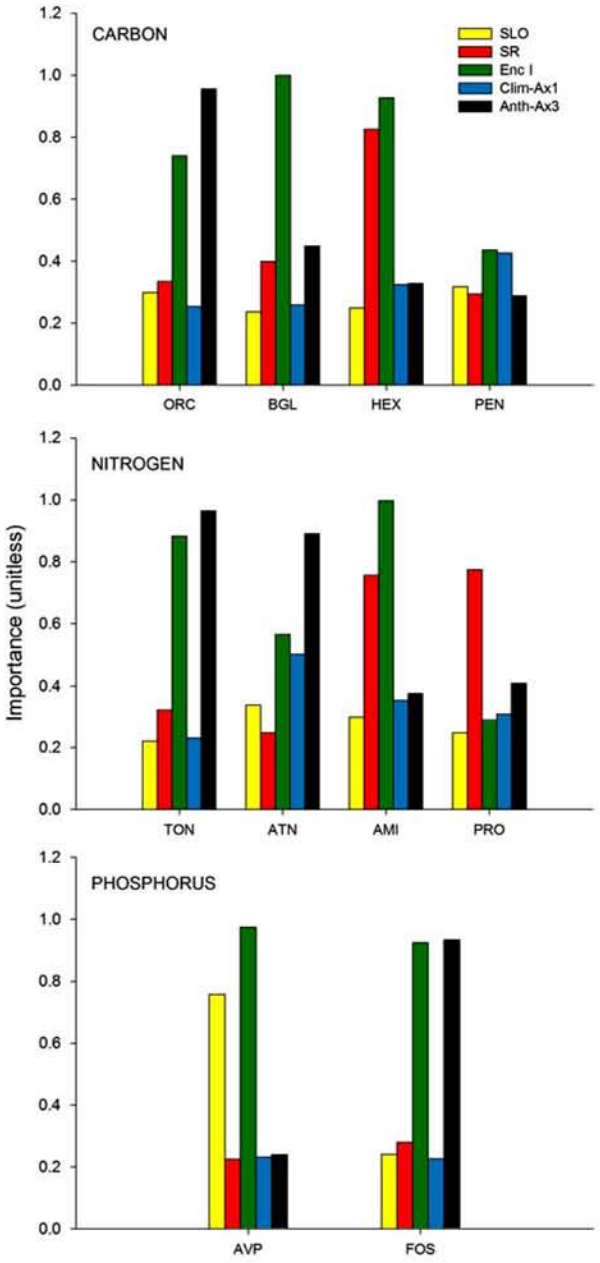

Figure 4. Relative importance of predictor variables in models of ecosystem functions of carbon, nitrogen, and phosphorus: ORC = organic carbon, BGL = β-glucosidase extracellular activity, HEX = hexoses, PEN = pentoses, TON = total nitrogen, ATN = total available N, AMI = amino acids, PRO = proteins, AVP = available inorganic phosphorous, FOS = phosphatase extracellular activity. The height of each bar is the sum of the Akaike weights (Wi) of all models that included the predictor of interest, taking into account the number of models in which each predictor appears. Variable abbreviations as in Table 1.

number of studies focused on the ecological consequences of this phenomenon (supplementary Figure S7). However, the literature is still dominated by studies focusing on single functional variables, such as soil C or aboveground net primary productivity. To our knowledge, our study is the first attempt specifically designed to directly evaluate in the field the effects and relative importance of shrub encroachment as a driver of ecosystem multifunctionality. In addition, two different vegetation types (that is, grasslands and shrublands) along a regional gradient have been studied, because the encroachment of sprouting shrubs has been observed not only in *S. tenacissima* grasslands, but also in shrublands dominated by the non-sprouter *R. officinalis* (supplementary Figure S1). Given that shrub encroachment in previously established shrublands has also been reported in other dryland regions (Noble 1997; Daryanto and Eldridge DJ 2010), our approach allows extending the generality of the potential effects of shrub encroachment in landscapes other than grasslands. Overall, our results showed that sprouting shrub encroachment, plant species richness and anthropic factors made important contributions to maintain ecosystem multifunctionality, this variable being higher in both grasslands and shrublands where sprouting shrubs appeared.

Contrary to our first hypothesis, we did not find an interaction between vegetation type and the presence/absence of sprouting shrubs. The magnitude of the functional changes promoted by the encroachment of sprouting shrubs was similar in both grasslands and shrublands dominated by an obligate-seeder shrub. Maestre and others (2009) hypothesized that one of the variables involved in the changes in ecosystem functioning promoted by shrub encroachment is the suite of traits of the encroaching shrub in comparison to that of the grasses being replaced. Our results extend this hypothesis to other shrubs that, similarly to grasses, are not functionally equivalent to the encroachers. *Quercus coccifera* is typically taller than *R. officinalis* and *S.tenacissima* (Blanca 2011). Larger shrubs provide more shade, reducing soil temperature, and subsequently increasing soil moisture (Maestre and others 2003). In this direction, Eldridge and others (2011) found a positive relationship between the height of the encroachers and improvements in ecosystem functioning. Similarly to height, *Q. coccifera* has a sprawling canopy and higher basal area than *R. officinalis* and *S. tenacissima* and, consequently, higher capacity for producing litter and higher retention of runoff and sediments (Cañellas and Miguel 1998). Thus, higher litter/debris mass and resource capture by *Q. coccifera* would be likely to promote higher levels of microbial decomposition, leading to enhanced C and N pools (McClaran

and others 2008; Throop and Archer 2008). This reasoning agrees with the observed increment in ecosystems functions related to these pools such as organic C and amino acid contents to name a few (Figure 2). Moreover, leaves of *Q. coccifera* have higher N, C, and protein contents than *R. officinalis*, whereas the latter has a higher caloric content, construction costs, ashes and lipids than *Q. coccifera* (Villar and Merino 2001). On the other hand, *S. tenacissima* leaves have a high fiber content (Bessadok and others 2007; Belkhir and others 2012), and typically show lower N contents than *Q. coccifera* leaves (Maestre and Cortina 2006). *Stipa tenacissima* and *R. officinalis* have higher foliar C:N ratios than *Q. coccifera* (Ferran and others 2005; Maestre and Cortina 2006), and this may lead to higher decomposition rates (Zhang and others 2008) of the litter of *Q. coccifera*. Thus, the differences in important functional traits between *Q. coccifera* and both *R. officinalis* and *S. tenacissima* may underlie the enhancement in ecosystem multifunctionality observed after the encroachment of grasslands and shrublands by *Q. coccifera*.

Results of the model inference approach showed that species richness and the third anthropic PCA component (*Ant-Ax3*) also explained an important part of the variation found in the *M*, *C*, *N*, and *P* indices, as well as in most ecosystem functions, as we stated in our second hypothesis. Regarding plant species richness, the relationship between this predictor and these indices was positive in all cases. It has been suggested that biodiversity may be one of the major drivers of ecosystem changes in the 21st century (Hooper and others 2012), and results reported here support this statement given the positive change in ecosystem multifunctionality observed with increases in species richness. These results are similar to those found in Maestre and others (2012a), where multifunctionality was positively related to species richness in global drylands comprising multiple vegetation types. In our study sites, one could expect that this positive richness–function relationship is mediated by nucleation processes mediated by *Q. coccifera*, given the attraction that this species exerts on birds that feed on its acorns and disperse other endozoochorous seeds when perched (Verdú and García-Fayos 1996; Bonfil 1998; Gómez 2003). Alternatively, stronger facilitative effects of *Q. coccifera* compared to those of *R. officinalis* and *S. tenacissima* could be due to the better soil conditions provided by the former (that is, higher available N in *Q. coccifera*; Supplementary Figure S2), which contribute to an increase of species richness at the entire community level (Soliveres and others 2011). However, the lack of correlation between species richness and the cover of sprouting shrubs (Pearson's, $r = 0.08$, $n = 44$, $P = 0.6$) may exclude nucleation processes as a potential explanation of the patterns observed. This lack of relationship between species richness and shrub cover contrasts with other studies showing negative (Selene and Collins 2008; Ratajczak and others 2012), positive (Cabral and others 2003) or negative and positive (Dickie and others 2011) relationships between both variables, and supports that the encroachment effects on diversity should not be generalized among different ecosystems.

In addition, our modelling approach also showed that anthropic factors had negative effects on multifunctionality (Table 2, supplementary Table S6). The *Ant-Ax3* component was positively related to the *M* index and distance to roads, meaning that higher ecosystem multifunctionality was found at sites in which roads were more distant. These results followed our expectations, given the strong effects of past human uses on the Mediterranean Basin (Blondel 2006), and previous studies showing that ecosystem properties depend to a large extent not only on biotic, but also on anthropic effects (Hooper and others 2005; García and Martínez 2012). What is most surprising here is that, despite that the variables selected here as proxies of human impacts were indirect measurements, they explained a significant part of the variation in multifunctionality. In fact the removal of the *Ant-Ax3* component as a predictor variable substantially reduced the fit of the model adjusted to *M* (Table 1). More accurate data regarding fire frequencies, grazing and/or harvest intensities per plot would have been even better predictors of ecosystem functions, but these data were not available for our sites, as the consulted historical archives did not have the spatial resolution required for the approach followed here. Nevertheless, it is important to note the fact that direct, "on-site" measurements such as encroachment and plant species richness had similar importance as indirect measurements of human impacts. Such measurements, which are easy to obtain and—as shown by our results—informative, offer great promise to improve our knowledge on the factors affecting ecosystem structure and functioning, particularly in those ecosystems with a long history of human use.

Regarding climate, it has been shown that increases and decreases in temperature and precipitation, respectively, can reduce ecosystem multifunctionality in global drylands (Maestre and others 2012a). In our work, multifunctionality

tracks these trends. However, the effect of climate was surprisingly less important than that of encroachment, species richness and anthropic factors. This is likely due to the relatively narrow gradient of precipitation and temperature existing among the studied sites (supplementary Table S1). Effects of small-scale variables on ecosystem functions may be more important than large-scale climatic variation. Indeed, the level of encroachment and species richness, which are within-site variables more directly related to soil processes (García-Fayos and Bochet 2009), were the most important variables driving ecosystem multifunctionality.

In summary, we conclude that the encroachment by sprouting shrubs enhances ecosystem multifunctionality in semi-arid Mediterranean grasslands and shrublands, and that both shrub encroachment and species richness were the most important drivers of ecosystem functioning and multifunctionality along the environmental gradient studied. Our study is the first documenting that ecosystem multifunctionality in shrublands is enhanced by encroaching shrubs differing in size and leaf attributes. Our findings reinforce the idea that encroachment effects on ecosystem functioning cannot be generalized, and that are largely dependent on the traits of the encroaching shrub relative to those of the species being replaced.

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